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Source: Journal of Herpetology, 46(2):213-220. 2012.
Published By: The Society for the Study of Amphibians and Reptiles
DOI: http://dx.doi.org/10.1670/11-327
URL: http://www.bioone.org/doi/full/10.1670/11-327

Journal of Herpetology, Vol. 46, No. 2, 213–220, 2012

Long-Term Growth of Desert Tortoises (*Gopherus agassizii*) in a Southern Nevada Population

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Abstract.—**Knowledge of growth rates, age at maturity, and longevity are important aspects of a species life history and are directly applicable to life table creation and population viability analyses. We measured the growth of a cohort of 17 semi-wild Desert Tortoises (*Gopherus agassizii*) located in Rock Valley, Nevada over a 47-yr period beginning in 1963. The tortoises were initially marked as hatchling and juvenile animals between the years 1963 and 1965 and ranged in size from 47 to 77 mm in plastron length. We assigned ages of 1–4 yr to the tortoises at initial capture based on their body size. These tortoises were recaptured, measured, and weighed approximately annually since their initial capture. Growth of male and female tortoises did not differ significantly until animals reached the age of 23–25 yr. Annual tortoise growth was correlated with the production of ephemeral vegetation, while accounting for size, sex, and repeated measurements of the animals as well as the interval between measurements. However, the production of ephemeral plants was likewise highly correlated (non-linearly) with winter rainfall. Stochastic predation events between 2003 and 2007 decimated this cohort of tortoises. The average age of the long-term surviving tortoises from this cohort was 43 yr with a range of 39–47 yr. Twelve of the tortoises survived to the age of 39 yr and 11 of the 12 reached 40 yr.**

The ability to accurately determine life history characteristics such as age, age at sexual maturity, expected life span, survivorship, mortality, and reproduction is paramount in characterizing at-risk populations and developing life tables, models, and population viability analyses. In this paper we address all the above life history parameters for the Desert Tortoise (*Gopherus agassizii*) except for reproduction. The Mojave population of the Desert Tortoise north and west of the Colorado River is federally listed as threatened by the U. S. Fish and Wildlife Service (1990). The body size of a Desert Tortoise is generally related to its age and, while long-term collection of data pertaining to age and growth of this cohort of tortoises has been reported (Medica et al., 1975; Turner et al., 1987), detailed knowledge of the growth of known-age Desert Tortoises beyond 26 yr of age is limited. Here, we document the long-term growth of a cohort of known-age Desert Tortoises from the Nevada Test Site (NTS), Rock Valley, Nye County, Nevada through the age of ~47 yr. Divergence between male and female Desert Tortoise growth is demonstrated and correlations with winter rainfall and ephemeral production are provided.

The Rock Valley cohort of Desert Tortoises were all initially marked when 47–77 mm in plastron length (PL) and conservatively aged at 1–4 yr of age. They were subsequently recaptured yearly between 1963 and 2007. The aging of Desert Tortoises, using scute annuli, was performed on this cohort of Desert Tortoises by Germano (1988); his age estimates were within 1 yr of what was perceived as the animals' known ages when they were 26 yr of age or less (Turner et al., 1987). Zug (1991) stated "Of all the age determination techniques, only ages derived from mark-release-recapture studies, and only from individuals marked as emerging hatchlings, are actual (true) ages. These actual ages are necessary to calibrate and/or verify the ages from all other techniques." Subsequently, skeletochronology has been used successfully to calibrate and corroborate age with a subset of this cohort of Desert Tortoises (Curtin et al., 2008).

Many sources estimate the life span of Desert Tortoises to range from 50–100 yr. Population viability analyses (Doak et al., 1994) and vital rate sensitivity analyses (Reed et al., 2009) have used these sources to parameterize their models. However, our study indicates this may be an overestimate of Desert Tortoise longevity, and this may have profound implications in our ability to predict long-term persistence of populations.

Understanding, and eventually reversing, the current downward trend in Desert Tortoise numbers will depend on our ability to understand the recruitment, population structure, growth, survivorship, and longevity of the species. These parameters are the basis for developing the accurate life tables and population viability analyses (Reed et al., 2009) which are needed to promote the recovery of the Desert Tortoise within different geographic populations.

Materials and Methods

Rock Valley is typified by a northern Mojave Desert mixed shrub community (Turner, 1973; Rundle and Gibson, 1996) dominated by creosote bush (*Larrea tridentata*), burro bush (*Ambrosia dumosa*), rhatanay (*Kramaria parvifolia*), and box thorn (*Lycium andersoni*). The valley is located at the southern boundary of the NTS along the northern slope of the Specter Range, 115 km northwest of Las Vegas, Nevada (latitude 46°43′N, longitude 116°11′W, and 1,020 m elevation). The NTS is a U. S. Department of Energy facility and has been used for nuclear weapons testing and a variety of other defense and energy related projects since its inception in January 1951 (Fehner and Gosling, 2000). The southern portion of Rock Valley was chosen by researchers in 1959 as a site to explore the long-term effects of ionizing gamma radiation on natural populations of plants and animals (French et al., 1974; Rundle and Gibson, 1996). Between 1962–1963, four (9 ha) study plots were established in Rock Valley (three fenced, one unfenced).

A cohort of 17 (1–4 yr old) immature Desert Tortoises, 47–77 mm in PL, were initially marked between 1963 and 1965 while researchers were meticulously searching each study area for lizards (Medica et al., 1975). The cohort of Desert Tortoises were periodically recaptured, measured, and weighed between 1966 and 1975 when they were encountered during annual mark–recapture studies of Western Whiptail Lizards (*Aspidoeilis tigris*). The 17 Desert Tortoises were aged to ±1 yr based on size in relation to other previously marked and recaptured Desert Tortoises. Each Desert Tortoise was measured (PL) inner notch to inner notch, and midline carapace length (MCL) was measured with a caliper to the nearest millimeter. Desert

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DOI: 10.1670/11-327

Tortoises were weighed with a spring scale to the nearest 25 grams. General health, time, location, and activity when first observed were noted. Desert Tortoises were marked permanently with notches filed into the edges of marginal scutes (Cagle, 1939). Temporary numbers were painted on the last vertebral scute in dark brown, quick-drying paint and a small (5 mm) color dot placed below the number to differentiate the year in which the animal was captured. Three larger tortoises of undetermined age (measuring 86, 95, and 97 mm in PL) also resided within the three fenced enclosures, and were periodically recaptured, but are not included in our analyses of growth of the known-age cohort.

Since 1982, we performed yearly searches for Desert Tortoises with the assistance of numerous volunteers. Each area was systematically searched during morning or late afternoon hours over 1 to 3 days in the spring (March–June) or autumn (September–November), or both. Following the listing of the Desert Tortoise as endangered (U. S. Fish and Wildlife Service, 1990), surgical gloves were worn when handling tortoises and field equipment was sanitized using 10% bleach solution after each use to minimize the potential spread of disease.

From 1963 through January 1991, precipitation data were collected at a rain gauge, located 50 m northeast of the center fenced area, by the National Oceanic and Atmospheric Administration (NOAA). The Rock Valley NOAA rain gauge was moved approximately 1.4 km north to a location along Jackass Flats Road on January 29, 1991 (R. Dennis, NOAA, pers. comm.) and has continued to operate at that location. Data were acquired from the National Climate Data Center website (http://www.ncdc.noaa.gov/). Rainfall in Rock Valley is typical of the eastern Mojave Desert, with the majority of precipitation occurring in December through March (Hereford et al., 2004). Localized thunder showers occur in July and August, with June being the driest month. Monthly precipitation was totaled for the period including October–March and is denoted as "winter rain" for each year. Winter ephemeral plants were measured in Rock Valley by a number of researchers over the past 40 yr (Beatley, 1969, 1974; Hunter, unpubl. data; and DeFalco, unpubl. data), providing measurements of ephemeral production in grams/m^2 for many contiguous years between 1963 and 2003 (Fig. 1). These production figures were incorporated into the analysis of tortoise growth. An analysis of ephemeral plant production as a function of winter rain was conducted using linear regression, where the log of plant biomass was entered as a dependent variable and winter rainfall was entered as the independent variable.

The average PLs of tortoises for each year of age were analyzed to determine if: 1) males and females grew at different rates; and 2) changes in individual growth rates occurring over time were associated with differences in available annual resources. Visual inspection of the data indicated an inflection point of reduced growth rate for each sex. To test for this, segmented regression was conducted separately for the average sizes for each age of males and females to identify the age at which growth rates differed. Growth rates (i.e., the slope of the line created by plastron vs. age) were compared for annual averages of males and females below and above the inflection point by ANCOVA, where PL was the dependent variable, age was a covariate, and sex was a factor.

To analyze Desert Tortoise growth as a function of the annual food resource, we analyzed all years for the annual growth of individuals as a function of seasonal rain and spring production of ephemeral plants; this was done using only tortoises with

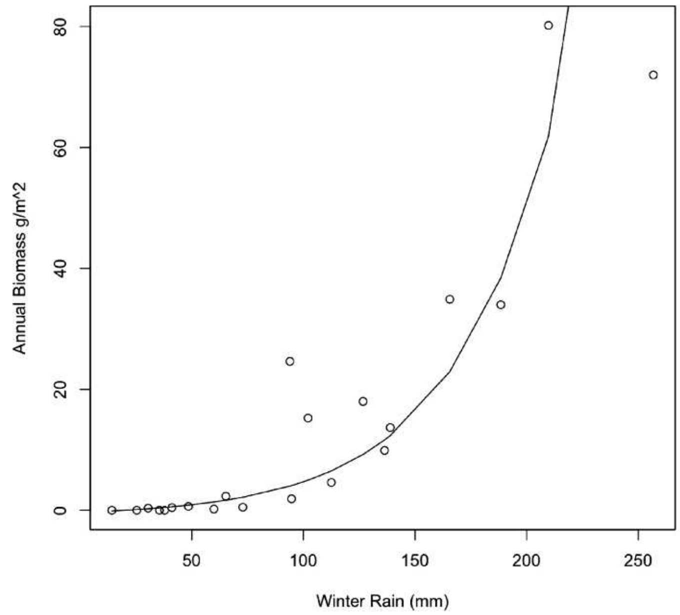

FIG. 1. Ephemeral production recorded in 21 different years between 1964 and 2004 in grams/meter^2 plotted against winter rainfall (October–March) for those years. The line represents the log-linear model fit with an $R^2 = 0.84$.

consecutive years of data and using the last measurement of the year for animals with multiple captures in a year. Animals were classified into two growth stages (i.e., immature animals below, and adult animals above, the segmentation point calculated above) to account for potential differential growth rates between immature and adult tortoises. A covariate was calculated to account for the differential time intervals (days) between measurements. Data were analyzed using a general linear model with mixed effects, where the animal number was treated as a random effect to account for repeated measurements of individuals over time using package nlme in R (nlme v. 3.1–96, R v. 2.7.1, R Development Core Team, 2007). Model selection was conducted using Akaike Information Criterion (AIC) values (Burnham and Anderson, 2001). To illustrate a measure of the goodness of fit for each model, a pseudo-R^2 was calculated by squaring the Pearson's correlation for the fitted models and growth (Zar, 1999; Table 1).

Desert Tortoise mortality was determined by finding the carcasses of marked animals when each study area was searched annually or by the lack of recaptures in successive years. Evidence of recent predation events was recorded within a few months of occurrence or during the next year's sampling event.

RESULTS

Precipitation.—The 45-yr average (1964–2008) annual rainfall by calendar year in Rock Valley was 160.2 mm with average winter rainfall (October–March) 107.05 mm. The range of fluctuations between high and low winter rainfall years varied greatly. Over the past 45 years, Rock Valley experienced winter rainfall exceeding 200 mm in 7 yr, 100–200 mm in 14 yr, 50–100 mm in 12 yr, and <50 mm (considered drought conditions) in 13 yr. Ephemeral production, generally considered "winter annuals" in the eastern Mojave Desert, had a positive non-linear relationship

TABLE 1. Models examined describing annual tortoise growth as a function of annual resource availability and covariates. A linear mixed effects model included animal ID as a random factor to account for repeated measurements of individuals. Model selection was conducted using AIC, and model weights (w_i) were calculated as in Burnham and Anderson (2001). Pseudo-R^2 was calculated as the squared Pearson correlation coefficient between growth and the predictions of the fitted model.

Model	AIC	ΔAIC	w_i	Pseudo-R^2
Rain + Days + Class	1206.74	0.00	0.95	0.50
Days+ Class	1214.15	7.40	0.02	0.44
Rain + Days + Class + PL	1214.72	7.98	0.02	0.50
Rain + Days + Class * PL	1217.41	10.67	0.00	0.50
Rain + Class	1220.64	13.90	0.00	0.42
Class	1224.43	17.69	0.00	0.37
PL + Class	1233.49	26.75	0.00	0.37
PL	1249.31	42.57	0.00	0.33
Days	1292.97	86.23	0.00	0.21
Null	1293.06	86.32	0.00	0.16
Rain	1298.60	91.86	0.00	0.18

($R^2 = 0.86$, $t_{19} = 10.77$, $P < 0.0001$) with winter rainfall, with a marked increase in production above 100 mm of rainfall (Fig. 1).

Growth and Sexual Maturity.—The model that best predicted annual growth indicated that winter rain and ephemeral vegetation were equivalent predictors of the amount of annual growth of tortoises in sequential years. Because there was a richer data set for rainfall (Fig. 1), the analysis presented here uses that larger data set. The amount of winter rainfall was positively correlated with annual growth of tortoises ($t_{199} = 4.49$, $P < 0.0001$), as was the number of days between measurements ($t_{199} = 5.25$, $P < 0.0001$), and immature tortoises had higher annual growth rates than did adults ($t_{199} = 10.71$, $P < 0.0001$). This model had a 95% confidence that it was the best model, given the data relative to the other models tested, and the hypothesized interactions had little or no weight of evidence (Table 1). The mean annual growth of tortoises in millimeters declined with age, although growth spurts coinciding with high rainfall years were clearly evident (Fig. 2).

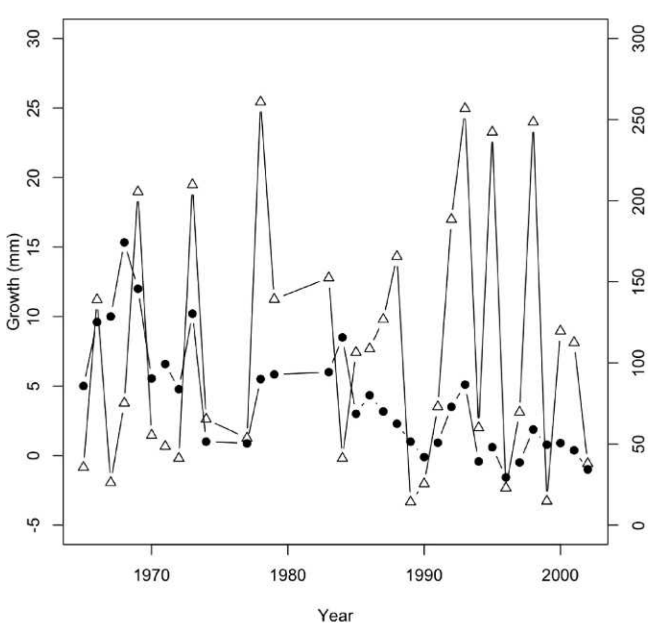

FIG. 2. Winter rainfall records for the 40-yr period of 1964–2003 in Rock Valley, Nye County, Nevada. Triangles indicate winter rainfall totals (October–March) and filled circles show mean tortoise growth in mm/year.

Growth of Desert Tortoises (both male and female) was linear and not significantly different between sexes (7.49 mm/yr and 7.03 mm/yr, respectively, $t_{43} = 0.15$, $P = 0.88$) up until ages in the early to mid-20s (age 25 for males and 23 for females). At these ages, there was a significant change in the growth rate for both sexes, and each had a different slope thereafter (1.5 mm/yr for males and 0.52 mm/yr for females, $t_{35} = 23.06$, $P < 0.001$). The incremental growth in PL of the surviving cohort of 17 Desert Tortoises from 1963 through 2009 is illustrated in Table 2.

We know that tortoises no. 6, 8, and 14 (in Table 2) were reproductive and possessed eggs when x-rayed in 1985, when their estimated ages were 23–24 yr and their PL lengths were 203–215 mm. We estimated that tortoises were sexually mature when they reached a minimum MCL size of ~190 mm (equivalent to 179 mm PL; Turner et al., 1986). Thus, our tortoises were estimated to be between 17–20 yr of age when they were ~177–179 mm PL (Turner et al., 1987). The six female Desert Tortoises of known age at Rock Valley reached sexual maturity between 16 and 21 yr, with the average age of 18.8 yr. At 30 yr of age, the differences between the size of males and females became statistically significant, and males continued to grow slowly while female growth was almost imperceptible (Fig. 3). The growth rate decreased significantly as Desert Tortoise age increased. There was one significant exception (no. 2, Table 2). The growth of this Desert Tortoise virtually ceased three times: once between the ages of 13 and 17 yr (139 mm PL) while other members of the cohort at 17 yr of age ranged in size from 162–207 mm (PL) for males and 160–180 mm (PL) for females; once between the ages of 19 and 20 yr; and again between 25–29 years (Table 2). This stunted Desert Tortoise remained smaller than all others in the cohort until its death in 1997 at the age of 34 yr, when it measured 181 mm MCL and 170 mm PL (Fig. 3).

Mortality and Predation.—Between 1963 and 1975, five Desert Tortoises were confirmed dead while two additional Desert Tortoises were last observed in 1969 and 1975 and were presumed dead. Five of these tortoises, 7–14 yr old, were last observed alive in years of low rainfall (1970–1972 and 1975–1977), and two Desert Tortoise deaths were recorded between 1995 and 1997 following the drought conditions of 1994 and 1996. Additional mortality took place between the late summer and early fall of 2003 when seven Desert Tortoises were found dead as a result of Mountain Lion (*Felis concolor*) predation (Medica and Greger, 2009). An additional known-age adult male Desert

TABLE 2. Plastron length (mm) based on last capture for the year and estimated age (years) of 17 Desert Tortoises (*Gopherus agassizii*) in Rock Valley, Nevada (1963–2008). Data from 1963–1987 are reported in Turner et al. 1987. (M = male, F = female, I = immature, D = animal found dead, X = animal missing.)

Animal Number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Sex	M	F	M	M	F	F	F	F	I	M	M	I	M	F	I	I	F
Age (years)																	
1	49	47															
2			51	53	54	55											
3		61		56		65	61	66	66	66	68						
4					83		68	71	71	80	72	71	71	73	74	77	77
5				77		83		79	83	87			74		92	80	
6					108				86	97				101	97	91	
7	108		112	110		112	95	104	119	114			96			105	119
8	119		117	112	122	116	111	106	129	116				115	124	120	124
9	123		118	120	130	129	120	108	134	123	120		127	127	126		128
10	135	120	128	129	132	133	122	114	138	130	121	113	128	133	131		132
11			132	143		146	124		146	136	126	113	133	139	134		147
12				146		147		134	147	138	133		138	147	142		
13	152	139	149		158			136	157				152				
14	153	139	149		157	168	147			150	143						
15	156	139	163		165	169	147			152			162	162			
16	170	139	165	201	167	174	154	159		157	157		167	166			195
17	176	139	174		170	177	160			162				168			
18										167			207	180			
19	188	145	179		185									180			
20		145	191		194	193	177										208
21		148	205			200					204			180			
22	209	151	215		213									188			
23		154		234	221	210	203			206							214
24	219	151	236		224	213		205		214	221			215			216
25	219	158	245	240	225	215				223			237	217			217
26		161		247	224	216	218	206		225	234			217			218
27	220	161	248	250	226	215	219			226	234			218			
28	221	161	252	250	224	216	220	206		226				222			218
29	227	162	272	250	226	215	219	205		231	238		251	220			219
30	229	166	282	251	228	215	219	205		234	241		251	219			221
31	225	168	283	262	226	219	221	208		244	247		253	219			
32	224	168	288	260	225	217	224	207		245			257	221			225
33	221		289	264	223	218	223				254			222			224
34	224	170	287	259	223	218	222	211		243	257		261	221			223
35	224	D	290	258	227	216	225	218		247	250		262	221			
36	226		291	261	224	218		221		247			258	221			
37	226		291	262	224	217	223			250	254		260	222			225
38	225		293		225	219	220			250			260	225			226
39	D		291	262	224	217	219			249	255		264	225			229
40			X		X	217	221	218		250			266	224			
41						D	221	221					267	224			
42							D						268				229
43				264						251	255			225			
44								D		X			D				
45				D							256			227			
46																	D
47											D			D			

Tortoise (no. 13, Table 2) was found partially consumed on October 15, 2004 and was killed or scavenged by a Kit Fox (*Vulpes macrotis*) or Coyote (*Canis latrans*), or both. In late September 2008, we documented a third major predation event. Between October 2007 and September 2008, six additional Desert Tortoises were preyed upon by Mountain Lions, as evidenced by the manner in which the carapace was ripped open and by the spacing of canine punctures. The last predation events differed from previous episodes, in that each of the three tortoise burrows had been excavated some distance beyond the burrow entrance (1–1.5 m), with a hole excavated straight down and intersecting the burrow tunnel, and with the Desert Tortoise extracted and lying nearby with the carapace broken open as described by Medica and Greger (2009).

DISCUSSION

Demographic patterns of long-lived species are often difficult to ascertain, as most studies are of short duration. The ability to estimate the ages of individuals based on their size may enhance the ability to understand demographic patterns of Desert Tortoise populations. We present 45 yr of capture–recapture data from the Rock Valley fenced plots. These data provide the only continuous record of growth in a known-age population of Desert Tortoises. These data show patterns of juvenile and adult growth, changes in growth that are concomitant with sexual maturity, and the responses of annual growth rates to ephemeral resources. In addition, the mortality recorded in this population indicates that life spans may be shorter than those typically assumed for Desert Tortoises, which

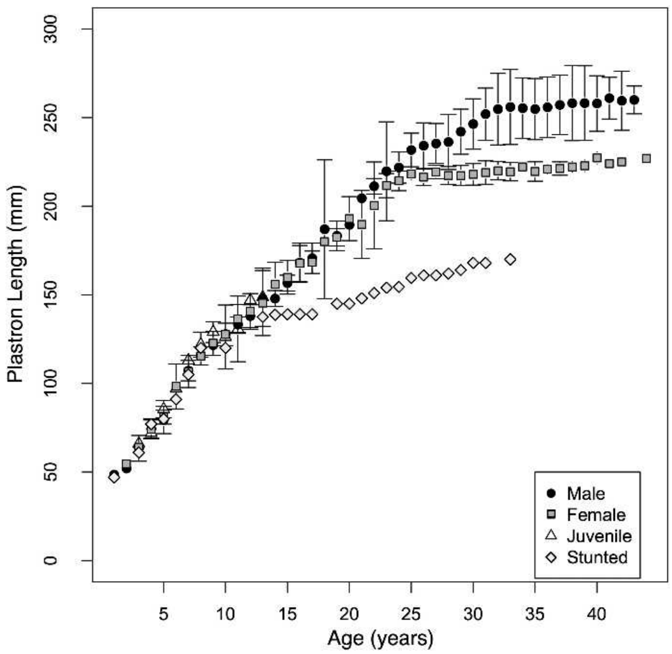

FIG. 3. Rock Valley male and female tortoise plastron length vs. age. The triangles represent juvenile tortoises which, after age 17 yr, is a single stunted tortoise (no. 2, Table 2) of known age (the diamond) that exhibited slower growth than the remainder of the cohort after the age of 13 yr. Error bars represent the 95% confidence interval of the mean.

may alter assumptions (or the use parameters) of population modeling and viability analyses.

Winter rainfall in the northern Mojave Desert promotes seasonal growth of ephemerals while summer rains produce few ephemerals in Rock Valley (Beatley, 1974) and, therefore, winter rain is a more accurate predictor of ephemeral forage and potential tortoise growth. A model by Turner and Randall (1989) and our data show a significant correlation between net primary production of ephemeral plants and "winter" rainfall.

Previous analyses of growth in this cohort of Desert Tortoises showed that growth of younger tortoises occurs primarily in the spring and early summer (Medica et al., 1975) and that growth rates appear to correlate with year-to-year fluctuations in winter precipitation. Significant germination of ephemeral plants generally requires a minimum 25 mm late September to mid-December rainfall (Beatley, 1967, 1969), and additional precipitation in late winter and early spring results in increased vegetative growth and survival (Beatley, 1974). Accordingly, Desert Tortoises in Rock Valley grew minimally in years where winter rainfall was less than 26 mm; for example, there was minimal growth during periods of drought (e.g., 1970–1973 and 1989–1990; Fig. 2). In this study, the years of greatest tortoise growth coincided with high winter rainfall and concomitant high ephemeral plant production (Rundel and Gibson, 1996; Hunter, unpubl. data). Growth of younger Desert Tortoises generally appears to be closely coupled to the timing of rainfall and subsequent forage production, as similar growth patterns have been reported in juveniles of other species of tortoises, e.g., Gopher Tortoise, *Gopherus polyphemus* (Landers et al., 1982), Spur-thighed Tortoise, *Testudo graeca* (Diaz-Paniagua et al., 2001), and Speckled Padloper, *Homopus signatus* (Loehr et al., 2007). Winter rainfall was also positively correlated with growth and density of the Side-blotched Lizard, *Uta stansburiana* (Turner et al., 1982), and the lack of winter rainfall resulted in the sharp decline in the *Uta* population of this annual species of lizard in Yucca Flat during drought years when reproduction was insignificant (Medica, unpubl. data). Similar results have been observed in small mammals (Kangaroo Rats, *Dipodomys* spp.) by Chew and Butterworth (1964) in Joshua Tree National Park and in Merriam's Kangaroo Rat, *Dipodomys merriami* and the Little Pocket Mouse, *Perognatus longimembris* (Saethre, unpubl. data) on the NTS.

Sexual maturity of Desert Tortoises has been inferred based on size and x-radiography in portions of the geographic range (Jackson et al., 1978; Turner and Berry, 1984; Turner et al., 1986) and has been estimated as 15–20 yr in the eastern Mojave Desert (Turner et al., 1987; Germano, 1989) and 11–22 yr (mean 17 yr; Curtin et al., 2009) and 13–14 yr (Germano, 1994) in the western Mojave Desert. In the Sonoran Desert, the estimated age of sexual maturity is 25–27 yr (Curtin et al., 2009). Growth curves for this cohort of Desert Tortoises show approximately linear growth until a point of inflection at approximately 23–25 yr, when males continued to grow and female growth slowed markedly. This growth pattern generally conforms to the curve presented by Germano (1994), which was based on the growth of carapacial scute rings for all five species of *Gopherus*. In contrast to our study, Landers et al. (1982) illustrated the growth curve for *G. polyphemus*, indicating that the growth of males slowed significantly at an age of approximately 16–18 yr while females continued growing through an age of 19–21 yr.

Based on previous and current data, it is apparent that the adult female Desert Tortoises in this data set show a slower, age-specific growth rate than do males post-maturity. Growth in females slowed at an age of 23 yr; this was slightly older than the age at maturity of 18.5 yr estimated for eastern Mojave populations from growth ring models (Germano, 1994). The Rock Valley females continued to grow slowly for a few years after sexual maturity; growth was estimated to be ~190 mm MCL based on Desert Tortoises from Goffs, California (Turner et al., 1986). Rock Valley Desert Tortoises reached ~190 mm MCL (179 mm PL) when their mean age was ~19 yr. Germano (1994) included the Rock Valley Desert Tortoises with tortoises of the western Mojave population. However, based on rainfall pattern, climate, and genetics (Hagerty and Tracy, 2010), the Rock Valley Desert Tortoises should clearly be considered as part of the northeastern Mojave grouping. The decline in growth rate in females as they reach sexual maturity could be attributed to the allocation of limited energy resources into reproduction rather than into growth (Wallis et al., 1999). Karl (1998) summarized the annual growth of adult males and females from Ward Valley, California in size classes (205–234 mm MCL), stating that the growth of female tortoises in these larger size categories was nearly negligible while males continued growing at a faster rate than females. While male Desert Tortoises do have larger home ranges than the females (Harless et al., 2009), and exhibit agonistic behavior (Berry, 1986) which appears to retard growth rates modestly, these characteristics are apparently not as energetically demanding as is allocating energy resources to produce eggs (Wallis et al., 1999).

Because Desert Tortoises are long-lived, approximate ages of the Rock Valley Desert Tortoises may be estimated using body length (MCL, PL, or both) with some reservation. One example is the stunted Desert Tortoise previously mentioned (no. 2, Fig. 2; Table 2) that did not grow much beyond the age of 13 yr and retained female secondary sex characteristics as it grew older. Another exception to the size and age axiom was presented by Curtin et al. (2009) for a Desert Tortoise from the western

Mojave Desert; this animal was 125 mm MCL but was estimated to be 40 yr old using skeletochronological methods. We have no idea of the prevalence of these exceptions, but it is of note that in the Rock Valley cohort, one out of 17 Desert Tortoises (5.8%) could be misidentified, and in the west Mojave sample provided by (Curtin et al., 2009) one out of 69 (1.5%) may possibly be misidentified. Undoubtedly, the best method to determine ages of reptiles and amphibians is by either mark–recapture or skeletochronology (Halliday and Verrell, 1988; Zug, 1991).

Although there are records for captive terrestrial turtles living beyond 100 yr (Graham and Hutchison, 1969), the life span of wild Desert Tortoises has been estimated in popular literature on the World Wide Web (e.g., 50–80 yr, U. S. Fish and Wildlife Service, 2009; 80–100 yr, DesertUSA, 2009). However, the average life span reported in the scientific literature is approximately 40 yr for the majority of wild Desert Tortoises, with slightly over 50 yr given as a maximum age (Germano, 1992, 1994; Curtin et al., 2009) and now confirmed empirically in this work. While population viability analyses have been conducted by Doak et al. (1994), the U. S. Fish and Wildlife Service (1994), and Reed et al. (2009), these analyses relied largely on life tables developed primarily at the Goffs site in the eastern Mojave Desert (Turner et al., 1987; Berry et al., 1994; Reed et al., 2009). The three life table estimates developed by Karl (1998) have Desert Tortoises surviving to ages of 71–83 yr. The three oldest Desert Tortoises of known age included in the original Rock Valley cohort were 46 yr (a female) and 47 yr (a male and a female). The three larger unknown-age Desert Tortoises initially marked were likely older than the known-age cohort but did not live any longer. It is also arguable that the survivorship of these Desert Tortoises may have been enhanced by the fence, which may have kept terrestrial predators out, but this may be discounted by observations over the years of the presence of Kit Foxes and Bobcats (*Felis rufus*) within the plots (although Coyotes were often observed within Rock Valley but were never observed within the enclosures) and by the mortality due to predation that was recorded in later years (Medica and Gregor, 2009). It is likely that these mortality events were random and that the age of the Desert Tortoises selected simply reflected those that were available. How much longer these Desert Tortoises would have survived within the Rock Valley plots will never be known, but it is noteworthy that both male and female tortoises survived to approximately the same age and in equal proportions, averaging 43 yr, with some of the Desert Tortoises developing the concave carapace scutes that are presumed to be a sign of osteoporosis and possibly old age (J. Johnson, DVM, pers. comm.).

Significant mortality of localized Desert Tortoise populations has been documented over the past three decades in the eastern Mojave Desert from stochastic events such as predation and drought. For example, in Ivanpah Valley, California between 1981–1982, there was 18.4% mortality of radio-transmittered Desert Tortoises (Turner et al., 1984), and drought was also implicated as the potential cause of mortality of 24% of the adult tortoises in Piute Valley between 1979–1983 (Germano and Joyner, 1989). There was also a widespread drought in the Mojave from 1990 to 1995. High mortality was observed in Ivanpah Valley, California in 1995 following drought conditions in 1993–1994 that resulted in notably reduced production of ephemeral plants (Medica, Avery, and Lovich, unpubl. data). Within the same period, a number of dead and moribund Desert Tortoises were salvaged because of dehydration and starvation within the Mojave Desert of California (Berry et al., 2002) and in 1990, 41% of the population of telemetered Desert Tortoises monitored in Ivanpah Valley by Peterson (1994) died. Additionally, in Nevada during approximately the same time period (1995–1996), 30% mortality was observed at Cottonwood Cove due to lack of rainfall and production of ephemeral vegetation (Longshore et al., 2003). Finally, at the Red Cliff Desert Reserve near St. George, Utah, a 41–47% decline in the tortoise population was observed in 2003 which was primarily attributed to drought, although disease, habitat degradation, predation, and human-caused mortality may have also been responsible (McLuckie et al., 2004). The most recent high mortality event, due primarily to coyote predation, occurred in the western Mojave Desert in the vicinity of Ft. Irwin, San Bernardino, County, California where a sizable proportion (21%) of 646 marked tortoises outfitted with radio transmitters were preyed upon by coyotes between March 2008 and December 2008 (Esque et al., 2010). There were also concurrent mortality events throughout the Mojave Desert in the same year, with site-specific mortality rates as high as 43%, indicating a regional pattern of elevated mortality (Esque et al., 2010).

With the prediction that hotter and drier conditions will prevail in the deserts of the southwestern United States (Breshears et al., 2005; U. S. Geological Survey, 2007), stochastic rainfall events and their frequency may play an increasingly important role in the long-term survival of threatened species such as the Desert Tortoise as climate change and the impacts of global warming advance. Under warmer and drier climatic conditions, Desert Tortoise populations may be severely impacted. Growth during the early stages of development may be slowed significantly due to reduced forage, resulting in a greater number of years being required to reach sexual maturity. Concomitantly, a retarded growth rate may result in increased predation (as individuals will be smaller and susceptible to predation for longer periods) and an increase in the generation time (presently estimated at 25 yr; U. S. Fish and Wildlife Service, 1994). Because tortoise activity is tightly coupled with temperature (Inman et al., 2009), warmer temperatures will alter the activity patterns of tortoises and may preclude above-ground activity in the daytime if temperatures are too high (Nussear and Tracy, 2007; Inman et al., 2009). Higher temperatures would also require Desert Tortoises to seek deeper or longer burrows to insulate themselves from high temperatures (e.g., above 42–43°C, which is the critical thermal maximum; Naegle, 1976). In some habitats, construction of deeper burrows may not be feasible because a caliche hardpan would preclude digging, although it would be possible to use or modify caliche caves typically found in wash banks. Germano et al. (1994) reported lengthy caliche burrows at the northern extreme of the range of the Desert Tortoise on the NTS that were up to 7.5 m in length, and tortoises in southern Utah are known to use deeper burrows in sandstone areas (Woodbury and Hardy, 1948; Nussear et al., 2007). Higher incubation temperatures may also influence the sex ratio of hatchlings, producing more females than males (Spotila et al., 1994), although this may create a positive influence on recruitment. Finally, the areas that are currently managed most intensively for tortoise conservation may not coincide with suitable habitat if climate change results in range shifts of the tortoise. Collectively, the impacts of climate change on populations of Desert Tortoises already in decline, in concert with the increasingly dominant human footprint in the region (Leu et al., 2009), may intensify the challenges of species recovery.

Acknowledgments.—We wish to thank N. French for conceiving the Rock Valley study and F. B. Turner and J. R. Lannom Jr. for initiating the herpetological field studies in 1963 that have now spanned four and a half decades. Data collection between 1981 and 2009 was possible through the participation of volunteers, especially P. Greger, K. Murphy, M. Burroughs, and J. Burroughs and numerous additional individuals from the following organizations: Bechtel Nevada; Bureau of Land Management; EG&G Energy Measurements; National Security Technologies LLC; Reynolds Electrical Engineering Co., Inc.; Smithsonian Institution; Student Conservation Association; U. S. Department of Energy; U. S. Fish and Wildlife Service; U. S. Geological Survey; U. S. International Biological Programme; University of California, Los Angeles; University of Nevada, Las Vegas; and University of Nevada, Reno. We also thank the U. S. Department of Energy, Nevada Operations Office for continued encouragement, access to the study site, and support that has enabled the collection of such an irreplaceable data set. We also thank L. DeFalco for providing unpublished ephemeral biomass data. K. Dodd, B. Henen, D. Wilson, A. Malisch, B. Halstead, K. Berry, K. Phillips, and several anonymous herpetologists reviewed earlier drafts of this manuscript and we thank them for their comments. A Nevada Department of Wildlife Scientific Collection permit was obtained for each year that measurements were recorded. A U. S. Fish and Wildlife Threatened Species permit, Number TE759747, was issued to PAM, which was required after the federal listing of the Desert Tortoise in 1989. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U. S. government.

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Accepted: 23 May 2011.